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MATING SUCCESS AND ALTERNATIVE REPRODUCTIVE STRATEGIES OF THE DIMORPHIC JUMPING SPIDER, *MAEVIA INCLEMENS* (ARANEAE, SALTICIDAE)

David L. Clark[1] and **Brandon Biesiadecki**[1,2]: [1]Department of Biology, Alma College, Alma, MI 48801, USA. E-mail: clarkd@alma.edu; and [2]Department of Physiology and Biophysics, Case Western Reserve University, School of Medicine, Cleveland, OH 44106, USA

ABSTRACT. The two male morphs of the dimorphic jumping spider, *Maevia inclemens*, differ dramatically in morphology and courtship behavior. The purpose of this study was to examine and compare the mating success of the two male types. Mating success was measured by the number and duration of copulation events, the latency of visual orientation by the female to a courting male, signals of female receptivity, risk of predation by the female, and the number of offspring produced by each morph. The morphs did not differ significantly with respect to copulation success, mating events, mating duration, signals of receptivity or the number of offspring produced. However, males did differ with respect to latency of visual orientation as a function of distance from the female. Near to the female, the gray males attracted female attention in significantly less time than tufted males. Conversely, at far distances from the female, the tufted males attracted female attention in less courtship time. This study suggests that males attain equal levels of mating success and that the two male morphs may have evolved alternative reproductive strategies for courtship at different distances from the female.

Keywords: Mating success, alternative reproductive strategies, jumping spider, dimorphism

Differences within a species for morphological and/or behavioral traits are relatively common in the animal kingdom. These polymorphic forms may evolve as a consequence of opposing selection pressures, producing differences in body size, coloration, physiology and behavior (Greene 1989; Futuyma 1986). Among the rarest forms of polymorphism is male dimorphism, the existence of two distinct male phenotypes within a single species, which has been documented in only a few animal groups (Wilson 1971; Gadgil 1972; Jenni 1974; Gadgil & Taylor 1975; Trivers 1976; Howard 1978; Endler 1980; Krebs & Davies 1987; Clark and Uetz 1992, 1993; Heinemann and Uhl 2000). Many studies suggest that dimorphic male phenotypes evolve via sexual selection through female choice, resulting in males with a particular phenotype being preferentially selected as mates (Darwin 1871; Fisher 1930; Gadgil 1972; Andersson 1982; Andersson 1994). Typically this leads to alternative reproductive strategies (Rubenstein 1980; Dunbar 1982; Arak 1984; Lott 1991) which are often attributed to phenotypic differences among males or their differential ability to compete for females (e.g., Reeves 1907; Le Boeuf 1974). However, in addition to sexual selection, distinct male phenotypes may evolve as alternative behavioral strategies (Howard 1978; Krebs & Davies 1987; Christenson 1984), or in response to environmental conditions that favor the use of one mating tactic over another (Reynolds et al. 1993; Moodie 1972). More rarely, genetic differences that predispose males to use a particular tactic (e.g., Lank et al. 1995) have also been reported.

There is considerable evidence that the courtship displays of males affect the mating decisions of females (see review by Andersson 1994) and variation among males typically leads to selection for males with the most desirable traits. Studies in which variation among males is discrete and the influence of interactions among individuals of the same sex is naturally absent can be especially useful for elucidating the evolution of divergent forms (Vinnedge & Verrell 1998). Hence, the presence of male dimorphism within a species provides a unique opportunity to assess the potential for different levels of mating success associated with alternative reproductive tactics.

To date there have been few investigations of male dimorphism and this is especially true for spiders. The most recent studies include Heinemann & Uhl (2000) reporting on male dimorphism in the linyphid spider *Oedothorax gibbosus* (Blackwall 1841) and Clark & Uetz (1992, 1993) and Clark (1994) on the dimorphic jumping spider, *Maevia inclemens* Walckenaer 1837 (also known under the name *M. vittata* (Hentz) Barrows 1918), a species exhibiting both morphological and behavioral dimorphism (Peckham & Peckham 1889, 1890; Painter 1913, 1914; Barnes 1955; Emerton 1961; Jackson 1982; Clark 1994). Given the advanced visual system of jumping spiders and its importance in reproductive behavior (Forster 1982; Jackson 1982), *M. inclemens* provides an excellent model system for investigating the mechanisms controlling male dimorphism, such as sexual selection through female choice or alternative male mating strategies (Gadgil 1972; Austad 1984).

The dimorphic jumping spider, *Maevia inclemens*, is found in the eastern and midwestern U.S.A. The "tufted" morph is entirely black in body coloration, has black pedipalps, white legs and three tufts of setae located on its anterior cephalothorax. In contrast, the "gray" morph is black and white striped in body coloration with a prominent white stripe above the anterior eyes, it has striped legs, bright orange pedipalps and it lacks the tufts (Clark 1994). Lacking tufts and orange palps, females are characterized by a rusty colored dorsal abdomen and a conspicuous white stripe below the anterior eyes (Barnes 1955; Kaston 1972).

In addition to morphological differences, the males differ in behavior during the initial phase (= phase I) of courtship (Clark 1994). The tufted morph stilts up on legs II–IV, raises and waves its first pair of legs back and forth and swings its abdomen side-to-side at an average distance of 9 cm from the female. The gray morph crouches in a prone posture, pointing legs I and II forward in a triangle-like configuration and sidles back and forth in front of the female at an average distance of 3 cm (Clark & Uetz 1993).

Previous studies of mate choice in *Maevia inclemens* have demonstrated that females tend to choose the male they see move first, independent of male morphology (Clark & Uetz 1992) and that as a function of different courtship distances, males present females with visual signals that are similar in size (Clark & Uetz 1993). These studies suggested that the different courtship behaviors of the two male morphs might represent alternative reproductive strategies for exploiting a movement bias in the mate selection system. Although it is known that females tend to choose the male they see move first, little is known about other aspects of male courtship behavior that might have an effect on the levels of mating success. The objective of this study was to determine if the two different male morphs of *Maevia inclemens* achieve equal or different levels of mating success. Similar to a study by Fernandez & Ortega (1990), the number and duration of copulation events and the number of offspring produced by each morph was used as a measure of mating success. Additionally, we scored the latency of visual orientation by the female to a courting male and how copulation events were terminated.

METHODS

Mature male and penultimate female *M. inclemens* were captured at several field sites in the local Cincinnati, Ohio (Hamilton County) area by hand and sweep net during the spring breeding season in June of 1995 and 1996. Voucher specimens have been deposited in the natural history collection at Alma College (Alma, Michigan). Spiders were maintained in the lab at Alma College and housed in cylindrical plastic deli containers, measuring 12 cm (d) x 4 cm (h). A diet of domestic crickets (*Acheta domesticus*) and fruit flies (*Drosophila* sp.) was provided on a weekly basis, and water was available *ad libitum*.

All observations of courtship behavior occurred between June and July of 1995 and 1996. Males and females were paired in a rectangular plastic arena, measuring 30 cm (l) × 15 cm (w) × 3 cm (h). A center partition separated the individuals during an acclimation period of approximately three min. The inner sides were lightly coated with petroleum jelly to keep the spiders from climbing out and escaping. Each female was randomly paired with an individual male (Total n = 55 females; with $n = 26$ tufted males; and $n = 29$ gray males). To control for previous mating experience, only virgin females (assessed by a final molt) were used. After the center partition was removed, spiders were allowed to freely interact until copulation termination or until the female rejected the male, whichever came first. Because females that decamp may be soliciting males to follow, rejection was defined as the female running away from the male three times and trying to escape out of the arena. In the event of no courtship, the individuals were separated after 12 min and were not tested again.

Each pairing was videotaped using a Panasonic HD 5100HS video camera and a Panasonic AG-1970 VHS format videocassette recorder. Subsequent to videotaping, the male and female interactions were scored for behavior frequency and duration using the "Observer" (Noldus Corp.) behavioral analysis program. Each interaction was scored for the following: a) Courtship—whether the male courted the female; b) Orientation latency–latency to female visual orientation of the courting male; c) Mating attempt—male tried, but did not successfully mount the female; d) Copulation—whether the male successfully mounted and copulated with the female; e) Female receptivity—females were scored for signaling to the male by either leg tapping or body posturing (see Clark 1994); f) Copulation events—number of copulation events per male; g) Copulation duration—the amount of time for each copulation event; h) Copulation termination—a score was given for how the copulation ended i.e., did the female force the male to dismount by attempting to dislodge it; or, did the male dismount voluntarily; and, did the female prey upon the male. For statistical comparisons, the chi-square test was used to test for differences among frequencies and the Wilcoxon sign rank test was used test for differences between sample distributions (reported as sample means).

Subsequent to a successful mating, females were maintained in the laboratory and allowed to construct egg sacs. The number of offspring resulting from each pairing was counted at the time of dispersal from the maternal egg sac. Since only virgin females were used, the offspring were the direct result of the interactions observed in the laboratory.

RESULTS

There were a total of 55 male and female pairings; 26 with tufted males and 29 with gray males. There was no significant difference in the number of males that courted females; 23 (88%) of the tufted males courted and 26 (89%) of the gray males courted ($\chi^2 = 0.02$, df $= 1$, $P > 0.05$; Table 1a). Only males that courted females were used in further analysis of mating success.

For males that courted, the latency to female visual orientation of the courtship display was measured. For all instances where visual orientation by the female was discernable, a significant difference in latency between the two male morphs was found (tufted $\bar{x} = 12.9$ sec, SD $= 3.68$, $n = 20$: Gray $\bar{x} = 9.84$ sec, SD $= 6.2$, $n = 22$; Wilcoxon test; $z = 2.33$; $P < 0.02$ Table 1b). Since Clark & Uetz (1993) and Clark (1994) reported that the males initiate courtship from significantly different distances from the female, tufted $\bar{x} = 9$ cm and gray $\bar{x} = 3$ cm respectively, an additional analysis of orientation latency to the courtship display was conducted. Here, the distance from the female was partitioned into two zones that covered the typical courtship range of the different males. The close zone was typical of the gray morph and ranged from 0 to 8 cm from the female. The distant zone was typical of the tufted morph and ranged from 8 cm and greater (maximum of 30 cm due to the length of the arena). In the close zone, the mean latency of visual orientation by the female toward the gray morph was significantly less than for the tufted morph (tufted $\bar{x} = 11.5$ sec, SD $= 3.47$, $n = 10$: gray $\bar{x} = 5.9$ sec, SD $= 1.69$, $n = 15$; Wilcoxon test; $z = 3.73$; $P < 0.001$; Fig. 1). However, in the distant zone, the advantage shifted to the tufted morph where the mean orientation latency toward tufted males was significantly lower than for gray males (tufted $\bar{x} = 14.3$ sec, SD $= 3.49$, $n = 10$: gray $\bar{x} = 18.14$ sec, SD $= 3.28$, $n = 7$; Wilcoxon test, $z = 1.92$, $P < 0.05$; Fig. 1). Interestingly, there was not a significant difference in orientation latency when the tufted individuals that courted in the close zone were compared to those tufted individuals that courted in the distant zone (Wilcoxon test: $z = 1.59$, $P > 0.10$; Fig. 1). However, when the gray males that courted in the close zone were compared

Table 1. Summary of the measurements of mating success for the two male morphs of *M. inlemens.*

	Tufted	Gray	Test	*df*	*p*	Power
a) Males that courted (n = 55)	23/26 (88%)	26/29 (89%)	$\chi^2 = 0.02$	1	>0.88	0.05
b) Mean female orientation latency (per males that courted)	12.9 s + 3.68 SD	9.84 s + 6.2 SD	$z = 2.33$		<0.02	0.47
c) Mean Mating Attempt (per males that courted)	3.34 + 2.63 SD	2.53 + 2.26 SD	$z = 1.07$		>0.2	0.17
d) Number of Males to Copulate (per males that courted)	12/23 (52%)	14/26 (54%)	$\chi^2 = 0.014$	1	>0.90	0.05
e) Female Receptivity (per males that copulated)	10/12 (83%)	11/14 (78%)	$\chi^2 = 0.095$	1	>0.75	0.05
f) Mean Copulation Events (n = 59)	2.6 + 1.87 SD	1.9 + 0.82 SD	$z = 1.12$		>0.2	0.46
g) Mean Copulation Duration (n = 57)	5.6 s + 5.0 SD	5.1 s + 5.8 SD	$z = 0.71$		>0.4	0.07
h) Male Terminates Copulation (n = 52)	5/26 (19%)	3/26 (12%)	$\chi^2 = 0.59$	1	>0.44	0.05
i) Mean Offspring Produced	25.5 +8.2 SD	24.9 + 8.3 SD	$z = 0.0$		>1.0	0.06

to those individuals that courted in the distant zone, there was a significant difference in latency to orient (Wilcoxon test: $z = 3.69$, $P < 0.001$; Fig. 1).

Of the males that courted, not all successfully copulated and males often attempted to mate several times before the female allowed the male to mount. However, there was no significant difference in the mean number of mating attempts between the two male morphs (tufted $\bar{x} = 3.34$, SD = 2.63, $n = 23$: gray $\bar{x} = 2.53$, SD = 2.26, $n = 26$; Wilcoxon text: $z = 1.07$, $P > 0.2$; Table 1c). There was also not a significant difference in the number of males of either morph to copulate with female. For tufted males, 12 (52%) of the males copulated and for gray males, 14 (54%) of the males copulated with a female ($\chi^2 = 0.014$, df = 1, $P > 0.05$; Table 1d). Finally, females showed similar levels of receptivity towards the two male morphs. Of the males that copulated, 10 (83%) of the females' signaled receptivity to tufted males, and 11 (78%) of the females' signaled receptivity to the gray males ($\chi^2 = 0.095$, df = 1; $P > 0.05$; Table 1e).

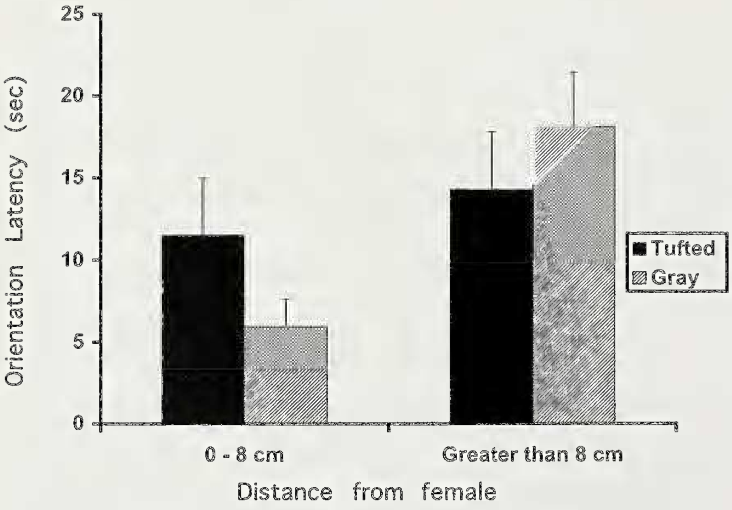

Figure 1.—Mean (+ SD) latency of female visual orientation to the courtship display of the two different male morphs of *Maevia inclemens* as function of distance. See text for statistical inference.

Since males often copulated more than once, the number of times that an individual male copulated was scored. There was no significant difference in the mean number of times that either male morph copulated with the female (tufted $\bar{x} = 2.6$, SD = 1.87, $n = 32$; gray $\bar{x} = 1.9$, SD = 0.82 SD, $n = 27$; Wilcoxon test: $z = 1.12$, $P > 0.2$; Table 1f). Likewise, there was no significant difference in mean copulation duration between the two male morphs (tufted $\bar{x} = 5.6$ sec, SD = 5.0, $n = 31$: gray $\bar{x} = 5.1$ sec, SD = 5.8, $n = 26$; Wilcoxon test: $z = -0.71$, $P > 0.4$; Table 1g).

Copulation generally terminated when the female tossed the male up, pushed him away and lunged in an attempt to capture the male. Females terminated copulation events significantly more often than males (female terminates = 85%; male terminates = 15%; χ^2 = 54.87, df = 1, $P < 0.001$). However, there was no significant difference in copulation termination frequency between the two male morphs (tufted male terminated = 19%; gray male terminated = 12%; χ^2 = 0.59, df = 1, $P > 0.05$; Table 1h). For all males that courted, one tufted male was preyed upon and no gray males were cannibalized in these observations.

As a final assessment of mating success, the number of offspring that dispersed from the maternal egg sac was counted. All females that copulated (tufted n = 12; gray n = 14) produced an eggsac and like most other assessments of mating success, there was no significant difference in the mean number of offspring produced by the two male morphs (tufted $\bar{x}$ = 25.5 spiderlings, SD = 8.2, n = 12: gray $\bar{x}$ = 24.9 spiderlings, SD = 8.3, n = 14; Wilcoxon test: z = 0.0; $P > 0.99$; Table 1i).

On a cautionary note, when there is failure to reject the null hypothesis, the possibility of a type II (β) error should be considered (Clark 1988). As a final analysis of the data, statistical power tests were conducted to determine the likelihood of making a type II error (see Cohen 1969). In general, the power results are consistent with our failure to reject the null hypothesis (summarized in Table 1). However, for (f) mean copulation events, the power results suggest some opportunity for a type II error.

DISCUSSION

In this study, mating success was measured in terms of time (i.e., latency of visual orientation by the female to a courting male and mating attempts); probable sperm transfer (i.e., copulation frequency and duration); displays of female sexual receptivity; risks associated with courtship and mating (i.e., orientation latency as a function of distance from the female and copulation termination); and lastly, the number of offspring produced by each male morph. With the exception of orientation latency as a function of distance, the results presented here indicate that the two male morphs of *M. inclemens* expend approximately equal amounts of time (and perhaps energy) courting and mating and ultimately produce equal numbers of offspring.

Almost all individuals of both male morphs courted the female in whose presence they were placed. Males generally began courtship by performing the morph-specific phase I courtship display (see Clark 1994) and almost all males that courted attempted to mate at least one time. For a mating attempt, the male would typically perform a zig-zag dance display or phase II (see Clark 1994) and move close to the female, touch her with legs I and attempt to mount. If unsuccessful, the male would move away and continue the phase II zig-zag dance display and then reattempt to mate until the female accepted or ran away. If the female ran away, the male usually chased and attempted to resume courtship. Both male morphs attempted to mate with the female an average of three times before they mounted the female successfully. It is likely that during these mating attempts females were assessing some quality about the male, however, they did not appear to treat the male morphs differently. This finding is supported by the equal number of males of each morph that received a signal of receptivity from females. These results support earlier studies on female receptivity where it was reported that females are equally receptive to the two different male morphs (Clark & Uetz 1992, 1993). Although many individuals were not successful at mating, there was no difference in the number of males of either morph that copulated with the female.

Not only did the same number of males of each morph gain access to females; the number of copulation events was approximately the same for both male morphs. Likewise, the duration of copulation was similar for the males, where each morph copulated for approximately five sec per copulation event. Although sperm volume was not measured directly, these results suggest that the two male morphs are transferring approximately equal amounts of sperm to the female (Jackson 1980). Likewise, with similar levels of sperm transfer, the number of offspring fathered by the two male morphs was not significantly different.

The two male morphs also appear to experience similar levels of predation risk from females. Results presented here demonstrated that females treated males equally with respect to copulation termination. In general, females ended a copulation event by attempting to toss the male off of her body. They did this by lifting their abdomen quickly and at the same time lifting the legs and lunging toward the male. Slow speed examination of videotapes revealed that females were attempting to capture the male while tossing it from their body. Both male morphs responded similarly by rapidly backing up (in less than a 1/30 sec) a centimeter or two from the female and then resuming phase II courtship.

Given the rather violent ending to mating, it might be expected that females would prey upon males more frequently. However, sexual cannibalism is relatively rare in this species. Clark (1992) and Clark & Uetz (1992) reported a frequency of approximately 2–3% of the males that court being preyed upon by the female. This is consistent with the current study in which one tufted morph was preyed upon. With such a small sample it is difficult to speculate on differences between the morphs. However, it is noteworthy that in this instance of sexual cannibalism, the tufted male had been performing phase I courtship approximately 4 cm from the female when she attacked. This suggests the possibility of different risks associated with morph-specific courtship displays as a function of distance from the female.

Another measure of risk associated with courtship display is the amount of time a male displays before being noticed by the female, or the latency of visual orientation. Since during phase I courtship males are attempting to attract female attention (Clark & Uetz 1992, 1993; Clark 1994) and the longer a male displays, the greater the risk associated with being spotted by visual predators. Although significantly different, overall, both males displayed for approximately similar amounts of time before the female visually oriented. The difference between the morphs becomes more apparent when courtship distance from the female was taken into account. At distances ranging from the female to 8 cm, gray males attracted female attention in significantly less time than tufted males within this same range. However, at distances ranging from 8–30 cm from the female (constrained by the length of the arena), tufted males attracted female attention in significantly less time than gray males in the same range. Clark & Uetz (1993) reported that the perceptual area of the displaying male decreases as a function of distance from the female. Therefore, it is possible that it takes a female longer to orient to the gray male at a distance because the corresponding size of the males' image is decreased. Or, it may be that the species specific morphological cues, such as orange pedipalps and the stripe above the eyes, have become obscured at a distance. Regardless, at a distance, gray males must display significantly longer than tufted males to attract female attention, providing evidence for the benefits associated with courting females from two different distances.

The results presented in this study suggest that the two male morphs of dimorphic jumping spider, *M. inclemens*, attain equal levels of reproductive success. However, some studies of alternative male mating tactics suggest a frequency dependent selection mechanism, which maintains the polymorphism (Rubenstein 1980; Austad 1984). In light of the data presented here, such a mechanism for *M. inclemens* remains elusive. A more plausible explanation for the maintenance of the two *Maevia* male morphs is a mixed Evolutionarily Stable Strategy or ESS (Maynard Smith 1988) where the polymorphism is genetic (Clark 1992) and each morph has evolved its own unique tactic with equal fitness. It is likely that sexual selection plays a role in balancing the dimorphism (Gadgil 1972) and that the two male morphs of *M. inclemens* represent strategies for exploiting different courtship distances from the female. Further study on the role of the morph-specific courtship behaviors, as a function of distance from the female, is required.

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